THE LIFE HISTORIES OF TWO BIRD TREMATODES OF THE FAMILY PHILOPHTHALMIDAE

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[Read 26th July, 1967]

Synopsis

Redial generations of *Cloacitrema narrabeenensis* n.sp. and *Philophthalmus burrili* n.sp. infect the digestive gland and gonad of the marine gastropod *Velacumantus australis*. These give rise to free-swimming megalurous cercariae which readily encyst on solid objects ; the cysts are oval in the case of *C. narrabeenensis* and flask-shaped in *P. burrili*. One experimental infection of *C. narrabeenensis* has been established in the bursa Fabricii of a young specimen of *Larus novaehollandiae* after feeding cysts ; *P. burrili* has been established experimentally in the ocular orbits of domestic chickens after feeding cysts, or direct inoculation of excysted metacercariae.

The natural definitive host of both species is *L. novaehollandiae*.

Introduction

At least six species of larval digenetic trematodes are known to infect the marine gastropod *Velacumantus australis* (Quoy and Gaimard) (Bearup, 1960). The life histories of three of these have been determined by Bearup (1956, 1960, 1961). The life histories of a further two species, which have very similar free encysting megalurous cercariae, but mature in widely different sites in the definitive host, *Larus novaehollandiae*, are reported here. A few details of both are as yet incomplete as free swimming miracidia, and experimental infections of snails with miracidia, have not been obtained. Further, excysted metacercariae of *C. narrabeenensis* have not been obtained.

Both species are members of the family Philophthalmidae and the taxonomy of this group has been recently discussed by Baugh (1962) and Penner and Fried (1963). *Philophthalmus burrili* n.sp. is of particular interest since its metacercaria could conceivably be infective to man. *P. lacrymosus*, which is normally parasitic in gulls, has been reported from the orbit of man in Belgrade (Markovic and Garzicic, 1939), and a further unnamed *Philophthalmus* species, from man in Ceylon (Dissanaike and Bilimoria, 1958).

Materials and Methods

Collections of *V. australis* were made at Narrabeen Lagoon, N.S.W., and Lake Burril, N.S.W. The snails were isolated in small plastic vials filled with sea water and infected specimens were detected by the presence of cercariae adhering to the surface film or swimming below the surface. Cercariae in the surface film readily encysted on small pieces of cellophane placed directly over them. Some specimens of *V. australis* released cercariae that formed oval cysts (cercariae of *C. narrabeenensis* n.sp.) while others released cercariae that formed flask-shaped cysts (cercariae of *P. burrili* n.sp.).

Twenty metacercariae enclosed in oval cysts were fed to a young silver gull, *Larus novaehollandiae*. Oval cysts were also fed to two mice, two pigeons, and two domestic ducklings.

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Twenty metacercariae enclosed in oval cysts were fed to a young silver gull, *Larus novaehollandiae*. Oval cysts were also fed to two mice, two pigeons, and two domestic ducklings.

Varying numbers of metacercariae enclosed in flask-shaped cysts were fed to domestic chickens. Excysted metacercariae, readily obtained from flask-shaped cysts on transfer to 0·85% saline at 37° C., were inoculated directly into the orbit with a Pasteur pipette.

Adult gulls were obtained for autopsy from the vicinity of Narrabeen Lagoon to determine natural fluke infections.

Redial stages of both species were recovered from naturally infected snails by cutting off the terminal whorls of the spire and teasing out the digestive gland and gonad into sea water.

All stages recovered were examined alive and 0·05% neutral red in sea water was used as an intra-vital stain. 0·05% phenol red in sea water stained gland cell material in recently dead redia and cercariae of *P. burrili*.

Permanent balsam mounts were made of all stages recovered after fixing in either 10% formalin or 70% alcohol and staining with Gower's carmine. For temporary stained mounts of larval stages, aceto-orcein was used.

Drawings were made with the aid of a camera lucida and all measurements are in mms.

Observations on the Life History of *Philophthalmus burrili*, n.sp.

The genus *Philophthalmus* was established by Looss (1899) for a single species, *P. palpebarum*, from the conjunctival sac of *Corvus cornix* and *Milvus parasiticus*. Many species were subsequently described by various authors. Ching (1961) considered that of the 21 species described up to that time only nine were valid ; those falling as synonyms showed differences to valid species that could be assumed to lie within the limits of variation, and the remainder required to be examined in far greater detail to determine their validity. Baugh (1962) described two new species from birds in India, and Penner and Fried (1963) described the first species known to have larval stages in a marine snail. The latter authors implied that *P. skrjabini* was valid on the basis of type of vitellaria, and by reducing the genus *Ophthalmotrema* to synonomy with *Philophthalmus*, added a further species, *P. numenii*. However, as *P. skrjabini* was described from immature specimens, and the type of vitellaria is not necessarily constant for all species, it must at present be considered a *species inquirendae*. Oshmarin and Parukhin (1963) (quoted in *Helminthological Abstracts*, 1966) described *P. macrorchis* from a single specimen, but in view of Ching's work (1961), it seems better to regard this species as a *species inquirendae* as well. Cable and Hayes (1963) have claimed that *P. gralli* as described by West (1961) and Alicata (1962), from the U.S. and Hawaii respectively, is probably distinct from *P. gralli* Mathis and Leger, 1910, and they renamed the North American species *P. megalurus* (Cort, 1914). Thus, there now appears to be 14 valid species in the genus, excluding that described here.

Fisher and West (1958) were the first to determine the life history of a *Philophthalmus* species. Several life histories have been described since by a number of workers, and some studies on the biology of the flukes have been made by West (1961) and Fried (1962*a*, *b* and *c*).

Adult

(Fig. 4)

Mature specimens of *P. burrili* n.sp. bearing eggs were recovered from the nictitating membrane of domestic chickens between 13 and 49 days after feeding encysted metacercariae or inoculating excysted metacercariae directly into the orbit.

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The following description is based on 30 specimens ranging in age from 28 to 49 days, most of which had eggs containing miracidia with eyespots. The upper and lower limits of the measurements are the means for 28 and 49 days-old specimens respectively.

Description : Body elongate, slightly attenuated anteriorly, broadly rounded posteriorly. Cuticle lacking spines. In some specimens a slight constriction occurs near level of ventral sucker. Total length 2·8–3·7, greatest width 0·7–1·4 just posterior to ventral sucker. Forebody 30–35% of total length. Oral sucker subterminal, generally wider than long, 0·21×0·30–0·27×0·37 ; ventral sucker circular in outline, preequatorial, 0·4–0·55 ; ratio of transverse diameters of oral and ventral suckers, 1 : 1·33–1 : 1·38. No prepharynx ; pharynx muscular 0·25×0·24–0·30×0·28 ; gland cells (gc 2, Fig. 4) surround each end of pharynx ; oesophagus 0·15–0·25 but lacking in some specimens where forebody contracted ; caecal bifurcation 0·3–0·4 anterior to ventral sucker ; caeca long, extending to near posterior extremity.

Testes in hindbody, entire edges, tandem. Anterior testis oval, 0·30×0·35–0·40×0·55 ; posterior testis tends to be more pointed posteriorly, 0·25×0·40–0·50×0·55. Cirrus sac long and slender extending around left side of ventral sucker and reaching up to 0·2 into hindbody ; it contains a large seminal vesicle, long, extensible, finely spined cirrus, and some prostate cells. Genital pore median, close to caecal bifurcation.

Ovary spherical, median or displaced slightly to the left, 0·17–0·25 in diameter, may touch anterior testis. Uterus with many coils between anterior testis and ventral sucker ; distal portion runs alongside cirrus sac. Eggs non-operculate, slightly thickened at one pole ; dimensions given elsewhere (see p. 185). Vitellaria largely extracaecal, varying between tubular and follicular ; they form a conspicuous band along each side of body between 0·1 and 0·4 posterior to ventral sucker to ovarian level, where they run medially to terminate at a median vitelline reservoir. Large ovoid or sausage-shaped receptaculum seminis overlapping ovary and anterior testis seen in some specimens but apparently absent or not filled with sperm (thus not seen) in others ; its presence was correlated with presence of fertile eggs in uterus.

Excretory vesicle elongated, extending as far as anterior testis ; large longitudinal ducts extend anteriorly as far as oral sucker but finer excretory ducts not seen, and flame cell number not determined.

Hosts : Domestic chicken (Experimental), *Larus novaehollandiae* (silver gull) (Natural).

Localities : Lake Burril, N.S.W. (type locality) and Narrabeen Lagoon, N.S.W.

Type slides : Australian Museum, Sydney, Reg. No. W4158 (holotype and paratypes), School of Public Health and Tropical Medicine, Sydney, Reg. No. Mn 1567 (paratypes).

Remarks : Ching (1961) considered the following morphological characters of *P. gralli* fairly constant after examining more than 50 specimens from four different hosts : location of genital pore, ratio of transverse diameters of suckers, ratio of diameters of ovary and testes, type of vitellaria, extent of vitellaria, extent of seminal vesicle, and egg size. With the exception of type of vitellaria, which varies from follicular to tubular, and egg size, which differs between worms recovered from natural and experimental hosts, the same characters are essentially constant for *P. burrili* and have, therefore, been the main criteria used to distinguish *P. burrili* from other species. It is worth noting that the seminal vesicle may be transversely or vertically disposed posterior to the ventral sucker in *P. burrili*, and this results in some variation in its posterior extent. However, the overall length of the seminal vesicle remains constant.

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Philophthalmus species described in which the extent of the vitellaria is for 80–85% of the ventral sucker-anterior testis distance are *P. gralli* Mathis and Leger, 1910; *P. anatinus* Sugimoto, 1928; and *P. halcyonis* Baugh, 1962. However, Ching (1961) considered *P. anatinus* a synonym of *P. gralli*. *P. burrili* is very similar to *P. gralli* but differs from it in having smaller eggs and lacking cuticular spines. With the life history of *P. burrili* now known, other features, particularly the number of flame cells in the cercaria, 24 as against 36, distinguish it from *P. gralli*. Moreover, its redial stages occur in a marine gastropod as opposed to a freshwater gastropod for the rediae of *P. gralli*. *P. burrili* differs from *P. halcyonis* in that the seminal vesicle extends posterior to the ventral sucker, the ovary is considerably smaller than the testes, and the genital pore is at the level of the caecal bifurcation.

It is noted elsewhere that the size of eggs containing fully developed miracidia differs between worms recovered from the natural host (*Larus novaehollandiae*) and experimentally infected chickens. However, in the absence of any other feature which permits a clear distinction to be made, worms from these two sources are regarded as the same species. The difference in egg size may merely be the result of development in a different host. Moreover, while the size of mature eggs may be a fairly constant feature for some species developing in different hosts, Penner and Fried (1963) have noted differences of up to 25μ in the length of the eggs of *P. hegeneri* from five experimental hosts. This is a similar difference in egg length noted between specimens of *P. burrili* from the two sources mentioned.

Some worms were found in which eggs had not commenced embryonation. This was most noticeable in infections where only one worm was recovered. Further, in all specimens with infertile eggs a receptaculum seminis was not seen. This evidence suggests that cross fertilization is a necessary prerequisite to egg embryonation in this species. A similar phenomenon was noted in *P. hegeneri* by Fried (1962*a*) but the presence of infertile eggs in this case was not correlated with the absence of the receptaculum seminis.

After inoculating excysted metacercariae into the orbit of chickens the worms are located for two to three days near the opening of the lachrymal duct. They then move out from this region and attach to the internal surface of the nictitating membrane. The cuticle spines, present in the metacercariae, have disappeared after 12 days. By the time egg laying commences (i.e., after 13 days) and subsequently, the worms are found attached to the external surface of the nictitating membrane. In heavy infections of 12–15 worms little pathological damage is found apart from slight pressure atrophy and oedema of the epithelial cells which are pinched into the ventral sucker for attachment.

It was found that metacercariae inoculated into one eye sometimes migrated to the other. Presumably, this migration is made before the worms become attached to the external surface of the nictitating membrane.

Eggs

(Fig. 8)

Eggs in the distal coils of the uterus of adult worms contain well developed miracidia with eyespots. From adults established experimentally in chickens, the eggs are 0·09–0·095 long by 0·05 wide; from adults in naturally infected *L. novaehollandiae* they are 0·110–0·115 long by 0·06 wide. In some adults, eggs are apparently infertile; this has been referred to above. Newly formed eggs in the proximal coils of the uterus are 0·06 long by 0·03 wide. The eggs are thin shelled, lack an operculum, and may be "egg"-shaped or "sausage"-shaped, depending on movements of the enclosed ciliated miracidium. A small teat-like projection is present at one end of the egg. Each miracidium contains an active, elongated body, presumed to be the mother redia. Further details of the morphology of the miracidium have not been obtained.

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Rediae

(Figs 1 and 5)

The smallest rediae found in the digestive gland are about 1·5 long by 0·35 wide. A slight depression at the anterior end of each marks the position at the mouth; this is immediately followed by a mobile pharynx, 0·1 long. The caecum is prominent, approximately two-thirds the length of the redia, and contains yellow pigmented granules, probably derived from digestive gland tissue. The lumen of the redia is empty at this stage, apart from germinal tissue in the posterior region. A distinct prolongation of the posterior end, termed caudal appendage, is present. The birth pore is slightly elevated, 0·3 from the anterior end, while the lappets are more prominent, 0·4 from the posterior end. No collar was located.

Larger rediae, containing many developing cercariae and germ balls throughout the lumen, are up to 5 long by 0·8 wide. Slight yellowish pigmentation of the body wall is seen in some specimens. The caudal appendage is prominent and birth pore and lappets are at approximately the same relative levels as in small rediae. The pharynx and caecum are essentially the same size as in small rediae and the caecum is similarly pigmented and packed with solid matter.

Rediae are quite active when freed from snail tissue.

Cercaria

(Figs 2, 3, 17 and 18)

Infection rates of *V. australis* with *Philophthalmus* cercariae in Lake Burril were low (1–2%) over the study period (latter half of 1966 until March, 1967). The incidence was determined by natural emergence of cercariae which is probably below the true incidence for this locality. From Lake Narrabeen, 29 snails out of 3,565 were found infected with *P. burrili* between 1954 and 1959. These figures were obtained from examining crushed snails. Experiments to determine the effects of salinity on emergence have not been carried out. Rarely, double infections of *P. burrili* with either *Austrobilharzia terrigalensis* Johnston, 1917, or *Acanthoparyphium spinulosum* Johnston, 1917, were found, and on one occasion a triple infection of *P. burrili* with *Stictodora lari* Yamaguti, 1939, and *A. spinulosum* was encountered.

The cercariae are active but not progressive swimmers. Their chief movement is a flexing of the body and tail, which are then straightened by a sudden flick. This may elevate them slightly, but they never appear to progress in any particular direction. Most cercariae eventually reach the surface and they may hang there limply, supported by an air bubble enclosed by the ventral sucker (Fig. 17), or lie horizontally in the surface film either at rest, or swaying from side to side (Fig. 18). Some cercariae attach to the bottom of the container by the sucker-like organ at the tip of the tail. When drawn up into a Pasteur pipette the cercariae adhere to the inner glass wall and readily encyst.

In immature cercariae, gland cells (gc 1, Fig. 2), containing granular material, are arranged in four distinct longitudinal rows between the oral and ventral suckers. Posterior to the ventral sucker the rows are not as conspicuous and they appear to terminate abruptly 0·05 from the posterior end of the body. The remaining portion of the body contains less densely granular material. Prior to being released from the redia, the contents of these cells are secreted to form a jacket around the entire body apart from the suckers (Fig. 3). This makes the body of the cercaria considerably less opaque. It is interesting to note that dilute phenol red does not stain the jacket until the cercaria dies. This suggests that the jacket is enclosed by a living membrane (probably comparable with the embryonic epithelium in *Fasciola hepatica* cercariae described by Dixon, 1966) since these are impermeable to phenol red.

The average measurements of 10 free swimming cercariae, fixed in formalin, are: body, 0·60 long by 0·175 wide; tail, 0·300 long by 0·042; oral sucker,

Rediae

(Figs 1 and 5)

The smallest rediae found in the digestive gland are about 1·5 long by 0·35 wide. A slight depression at the anterior end of each marks the position at the mouth; this is immediately followed by a mobile pharynx, 0·1 long. The caecum is prominent, approximately two-thirds the length of the redia, and contains yellow pigmented granules, probably derived from digestive gland tissue. The lumen of the redia is empty at this stage, apart from germinal tissue in the posterior region. A distinct prolongation of the posterior end, termed caudal appendage, is present. The birth pore is slightly elevated, 0·3 from the anterior end, while the lappets are more prominent, 0·4 from the posterior end. No collar was located.

Larger rediae, containing many developing cercariae and germ balls throughout the lumen, are up to 5 long by 0·8 wide. Slight yellowish pigmentation of the body wall is seen in some specimens. The caudal appendage is prominent and birth pore and lappets are at approximately the same relative levels as in small rediae. The pharynx and caecum are essentially the same size as in small rediae and the caecum is similarly pigmented and packed with solid matter.

Rediae are quite active when freed from snail tissue.

Cercaria

(Figs 2, 3, 17 and 18)

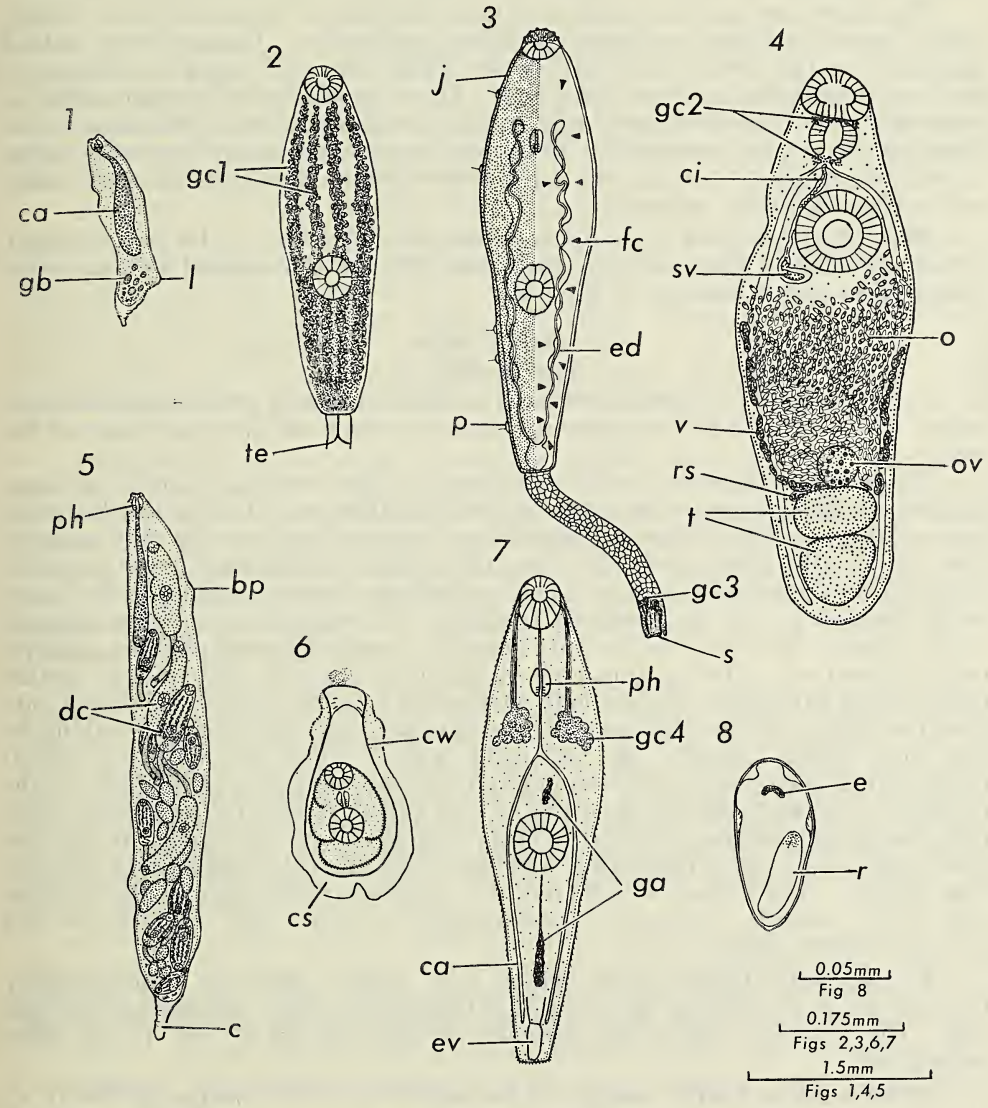
Infection rates of *V. australis* with *Philophthalmus* cercariae in Lake Burril were low (1–2%) over the study period (latter half of 1966 until March, 1967). The incidence was determined by natural emergence of cercariae which is probably below the true incidence for this locality. From Lake Narrabeen, 29 snails out of 3,565 were found infected with *P. burrili* between 1954 and 1959. These figures were obtained from examining crushed snails. Experiments to determine the effects of salinity on emergence have not been carried out. Rarely, double infections of *P. burrili* with either *Austrobilharzia terrigalensis* Johnston, 1917, or *Acanthoparyphium spinulosum* Johnston, 1917, were found, and on one occasion a triple infection of *P. burrili* with *Stictodora lari* Yamaguti, 1939, and *A. spinulosum* was encountered.

The cercariae are active but not progressive swimmers. Their chief movement is a flexing of the body and tail, which are then straightened by a sudden flick. This may elevate them slightly, but they never appear to progress in any particular direction. Most cercariae eventually reach the surface and they may hang there limply, supported by an air bubble enclosed by the ventral sucker (Fig. 17), or lie horizontally in the surface film either at rest, or swaying from side to side (Fig. 18). Some cercariae attach to the bottom of the container by the sucker-like organ at the tip of the tail. When drawn up into a Pasteur pipette the cercariae adhere to the inner glass wall and readily encyst.

In immature cercariae, gland cells (gc 1, Fig. 2), containing granular material, are arranged in four distinct longitudinal rows between the oral and ventral suckers. Posterior to the ventral sucker the rows are not as conspicuous and they appear to terminate abruptly 0·05 from the posterior end of the body. The remaining portion of the body contains less densely granular material. Prior to being released from the redia, the contents of these cells are secreted to form a jacket around the entire body apart from the suckers (Fig. 3). This makes the body of the cercaria considerably less opaque. It is interesting to note that dilute phenol red does not stain the jacket until the cercaria dies. This suggests that the jacket is enclosed by a living membrane (probably comparable with the embryonic epithelium in *Fasciola hepatica* cercariae described by Dixon, 1966) since these are impermeable to phenol red.

The average measurements of 10 free swimming cercariae, fixed in formalin, are: body, 0·60 long by 0·175 wide; tail, 0·300 long by 0·042; oral sucker,

0·05 in diameter ; ventral sucker, 0·08 in diameter. The body is constricted slightly at the ventral sucker level, and this is more noticeable in contracted specimens. Small, inconspicuous spines cover the cuticle. A number of small papillae, associated with blocks of refractile material, occur at the anterior end of the body. Along each side of the body there are five papillae with sensory " hairs ".



Philophthalmus burrili, n.sp.

1, Young redia ; 2, body of immature cercaria showing arrangement of gland cells ; 3, free swimming cercaria, body expanded, tail contracted ; 4, dorsal view of 49-day-old adult from nictitating membrane of experimentally infected chicken ; 5, mature redia containing developing cercariae ; 6, metacercaria within flask-shaped cyst ; 7, excysted metacercaria ; 8, fully embryonated egg from terminal part of uterus.

The mouth, surrounded by the oral sucker, leads into a moderately long prepharynx, 0·095, oval muscular pharynx, 0·040 long, long oesophagus, 0·090, and the caecal bifurcation is approximately two-thirds the distance between the anterior end and ventral sucker. The caeca extend to near the posterior extremity.

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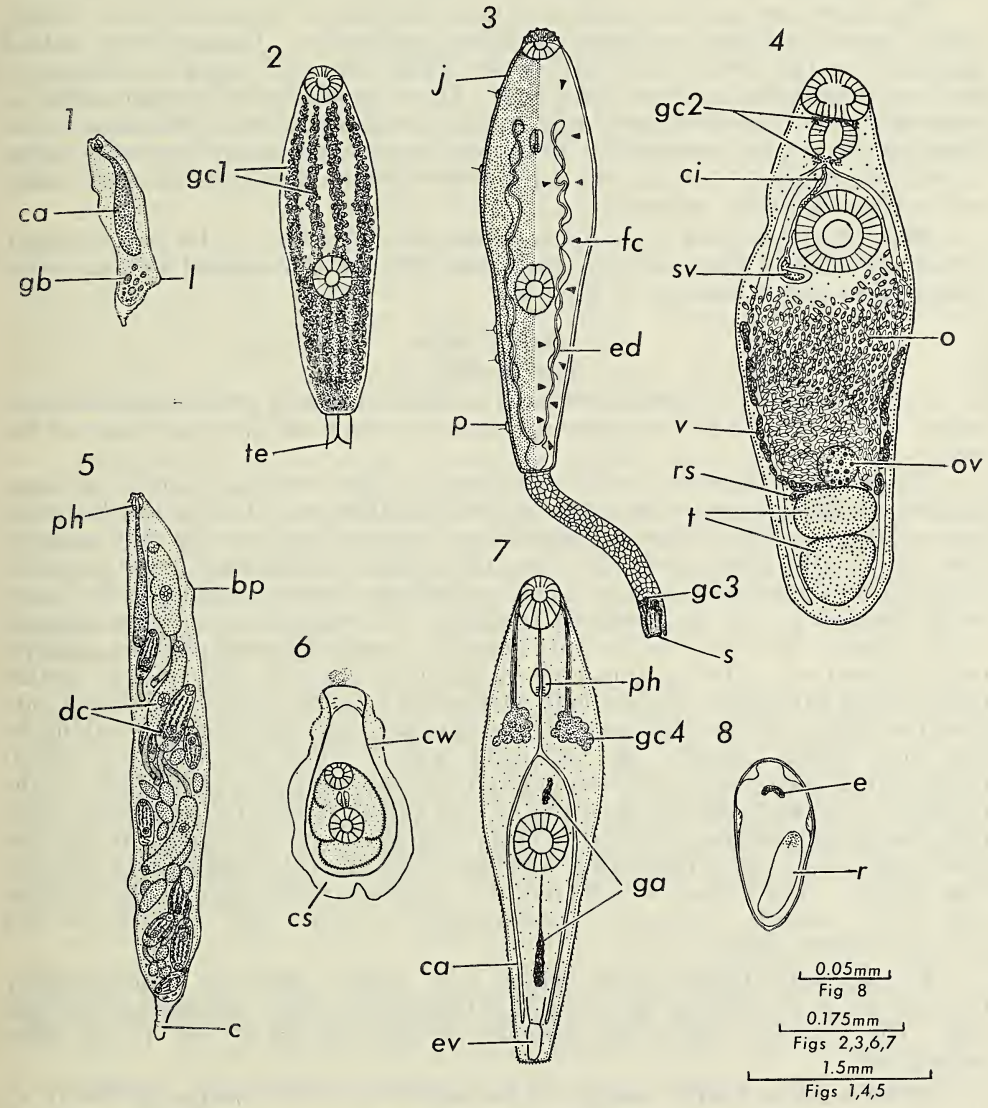

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A group of cells just anterior to the ventral sucker and a chain of cells between the ventral sucker and excretory vesicle represent the genital anlagen.

There is another group of cells on either side of the forebody between the pharynx and ventral sucker. Fine ducts from these cells run anteriorly and open on either side of the oral sucker. These cells are more clearly evident in excysted metacercariae (gc 4, Fig. 7).

The excretory system consists of a rectangular to ovoid excretory vesicle which varies in shape according to body movements. Lateral ducts extend anteriorly to the level of the oral sucker, where they turn back on themselves and run posteriorly into the hindbody. There appear to be 12 flame cells on each side, but finer excretory connections to these and the groupings of the flame cells were not determined. From the posterior end of the excretory vesicle a duct runs medially into the tail, forks 0·08 from the posterior end of the body, and each fork opens laterally.

The tail is occupied by vesicular parenchyma except at the posterior end. This is infolded to form a sucker-like organ, which is surrounded by four to six pear-shaped gland cells (gc 3, Fig. 3).

Metacercaria
(Figs 6 and 7)

Encystment of *P. burrili* cercariae is a relatively simple process as it involves, essentially, the body becoming free from the presecreted jacket and loss of the tail.

The cercaria attaches to the substrate by the oral and ventral suckers, flattens, and then contraction of the forebody commences. During the flattening process the so-called embryonic epithelium ruptures because the cyst material then stains with phenol red. Further, the rupture of this membrane probably allows mucoid substances to flow over the substrate, thereby cementing the jacket to the substrate. As the forebody contracts, the relatively fluid cyst material of the jacket, which overlies the body dorsally, is arched up and the open anterior end is closed off. During this process, the cyst material gels so that further contractions thus leave the forebody enclosed in a bulbous area. The hindbody then contracts into the bulbous area, the cyst material surrounding it having by this time gelled. Finally, the tail drops away. Thus, the resulting cyst is flask-shaped, the open end corresponding to the posterior end of the body of the cercaria. The metacercaria, as it can now be called, rotates in the bulbous area, but gradually becomes quiescent. There appears to be two layers to the cyst wall—one consisting of cementing substance, and the other making up the cyst wall proper. The former is indented at a point corresponding to the anterior end of the cercaria. Cysts are approximately 0·3–0·5 long by 0·175–0·234 at their widest point.

The enclosed metacercaria, which may remain alive for approximately three weeks, is identical to the cercaria but lacks the jacket, sensory papillae and tail. The cuticular spines and forebody gland cells (gc 4, Fig. 7) are more prominent.

Metacercariae excyst readily in sea-water or 0·85% saline at 35–37° C. Application of the temperature stimulus initiates very vigorous movements of the metacercaria which escapes from the open end of the cyst, anterior end foremost. By comparison with the cysts of *C. narrabeenensis*, cysts of this species do not tan.

Observations on the Life History of *Cloacitrema narrabeenensis*, n.sp.

The genus *Cloacitrema* was established by Yamaguti (1935) for a single species, *C. ovatum*, from the cloaca of *Bucephala clangula clangula*. McIntosh (1938) added *C. michiganensis* from the cloaca of the sandpiper, *Actitus macularia*

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One life history of a *Cloacitrema* species has been reported. Robinson (1952) found megalurous cercariae developing in an estuarine snail, *Cerithidea californica*, and encysting on the shell surface. The metacercariae developed to *C. michiganensis* in *Larus californicus*.

Adult

(Figs 12 and 15)

Thirty-five days after feeding 20 oval cysts to a young gull, four adult worms bearing mature eggs were recovered from the bursa Fabricii. Three specimens were examined in detail and the measurements of each are given. Mice, pigeons and domestic ducklings proved refractory.

Description: Body elongate, oval, constricted in middle, 3·3, 2·5, 2·2 long by 1·4, 1·15, 1·0 at greatest width and 1·2, 1·0, 0·9 at constriction level with ventral sucker; cuticle without spines. Oral sucker subterminal, 0·37 long by 0·53 wide, 0·16×0·41, 0·24×0·33; ventral sucker slightly pre-equatorial, 0·8 long by 1·00 wide, 0·40×0·68, 0·56×0·64; sucker ratios 1 : 1·7–2. No prepharynx; pharynx muscular, 0·40 long by 0·50 wide, 0·33×0·37, 0·35×0·27; oesophagus very short, less than 0·05; caecal bifurcation midway between posterior border of oral sucker and anterior border of ventral sucker; caeca long, narrow, ending in testicular zone.

Testes oval, entire edges, parallel or slightly oblique, close together or touching. Left testis 0·5 long by 0·2 wide, 0·3×0·3, 0·2×0·2; right testis 0·6×0·3, 0·25×0·24, 0·21×0·18; vasa efferentia join near level of ventral sucker and continue along left side of ventral sucker with the terminal point functioning as an external seminal vesicle. Cirrus sac oval, 0·3 long by 0·25 wide, 0·18×0·14, 0·19×0·16, terminating at a common genital pore ventral to posterior region of pharynx; it contains the distal end of the seminal vesicle, prostate cells and finely-spined cirrus.

Ovary spherical, 0·15, 0·11, 0·12 in diameter, median, approximately midway between ventral sucker and testes; oviduct short, joining a small spherical receptaculum seminis at left of ovary and transverse vitelline duct, and then continues to uterus. Vitelline follicles compact, about five or six on each side between ovary and testes, dorsal to caeca. Uterus long, folded transversely to occupy posterior half of body but without coils in pre-ventral sucker zone; terminal portion thin walled, rugose, lying alongside seminal vesicle and opening at common genital pore. Eggs in last few coils have oculate miracidiae. Egg sizes given elsewhere (see p. 190).

Excretory vesicle elongate oval with short duct opening posteriorly. Two main anterior ducts leave antero-laterally and continue forwards around edges of testes to pharynx level. These ducts have several lateral outgrowths in this region. Finer excretory tubules not seen and flame cell number not determined.

Host: *Larus novaehollandiae* (silver gull) (Natural and Experimental).

Locality: Narrabeen Lagoon, N.S.W. (type locality) and Lake Burril, N.S.W.

Type slides: Australian Museum, Sydney, Reg. No. W4159 (holotype), School of Public Health and Tropical Medicine, Sydney, Reg. No. Mn 1377 (paratype).

Remarks: The closest relative of this species is *C. michiganensis* McIntosh, 1938, from which it differs in the following details:

(*a*) The close relation of the testes and their greater size;
(*b*) the wider separation of ovary from testes; and
(*c*) the larger pharynx. Similar differences exist between *C. narrabeenensis* and *C. oswaldoi* Travassos, 1940. In fact, the latter may well be a synonym of *C. michiganensis*.

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Eggs

(Fig. 16)

In the distal end of the uterus, each egg contains a fully developed miracidium with a prominent eyespot ; one free miracidium was seen in this position. Eggs are 0·070 long by 0·035 wide when immature, but those containing a mature miracidium are 0·120×0·067. The eggs are thin shelled, colourless to slightly yellow, broadly oval. The X-shaped eyespot of the miracidium is composed of numerous black granules. Each mature miracidium is ciliated, and contains an active, elongated, mother redia. An oval body is often found alongside the miracidium but its significance is not clear. Further details of the morphology of the miracidium have not been obtained.

Rediae

(Figs 9 and 13)

Rediae of two size groups are usually present in the digestive gland and gonad of infected snails ; the smaller are slender 0·4 to 0·5 long, translucent, with a prominent pharynx and relatively long gut (about 80% of the total length), a birth pore on a small teat-like elevation, and two prominent lappets. The birth pore is at about 25%, and lappets at 80% of the body length. Rediae of this type, but slightly smaller, 0·2 long, were found in the mantle tissue of one snail. Developing daughter rediae and cercariae were not seen in these small rediae, but germinal tissue could be located in the posterior regions of the body.

Larger rediae are 2·0 to 4·0 long and may contain up to 10 well developed cercariae, several younger ones and germ balls. The mouth has shallow lips ; it is followed by a large muscular pharynx and a caecum packed with yellowish matter probably derived from the digestive gland. The caecum is now only one-quarter to one-half the body length. The birth pore and lappets are difficult to see, although by rolling the redia under a coverslip they can be located.

Rediae actively bend and extend when freed from snail tissue.

Cercaria

(Figs 10 and 11)

Infection rates of *V. australis* with megalurous cercariae of *Cloacitrema* in Narrabeen Lagoon have been followed for five years (1954–1959) and have shown no distinct seasonal pattern. Infection rates rose with those of other common parasites (schistosomes, echinostomes and heterophyids) and sometimes reached 10% ; then they remained high for several months while other rates fell, or vice versa. These results were based on examinations of crushed snails ; cercariae emerge spasmodically from infected snails and thus figures obtained by isolating snails in small glass tubes and searching for cercariae are below the true incidence. In Lake Burril, the incidence was found to be 2–4% during the latter half of 1966 until March, 1967. Infected snails were seldom less than 30 mm. long, which is the size of mature snails (Ewers, 1963). Rarely, double infections of *C. narrabeenensis* with *Austrobilharzia terrigalensis* or *Acanthoparyphium spinulosum* were found.

Variations in the salinity of the lagoon water (from 50–90% that of sea water) did not appear to affect emergence. Cercariae live for 48 hours in lagoon water but die within an hour of transfer to fresh water.

Swimming behaviour and method of attachment to the surface film in *C. narrabeenensis* cercariae is essentially identical to *P. burrili* cercariae. (See p. 186 and Figs 17 and 18.) Further, cercariae encyst readily on the inner wall of a Pasteur pipette when picked up.

Various types of gland cells filled with cystogenous material obscure much of the internal structure of the cercarial body. In immature cercariae the gland cells are clearly in four longitudinal rows between the oral and ventral suckers.

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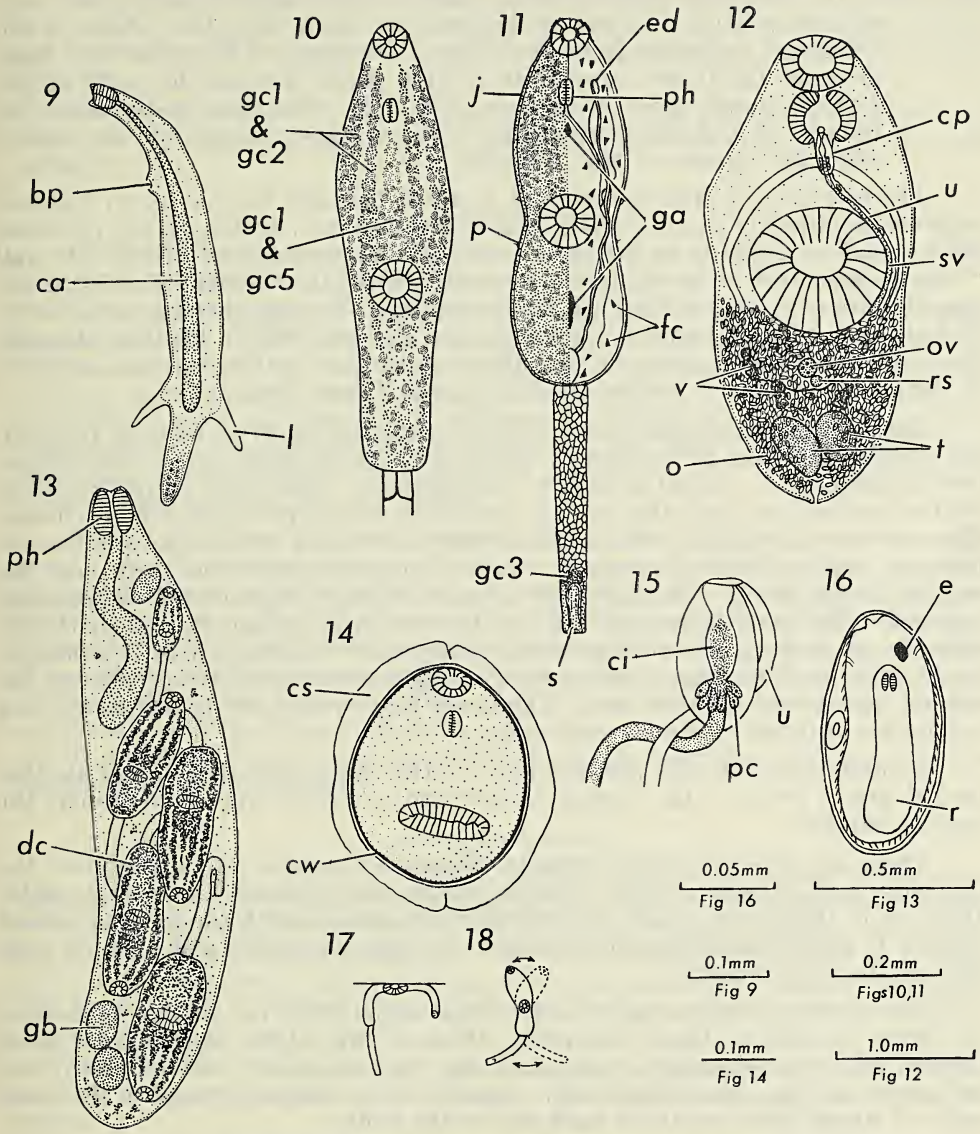

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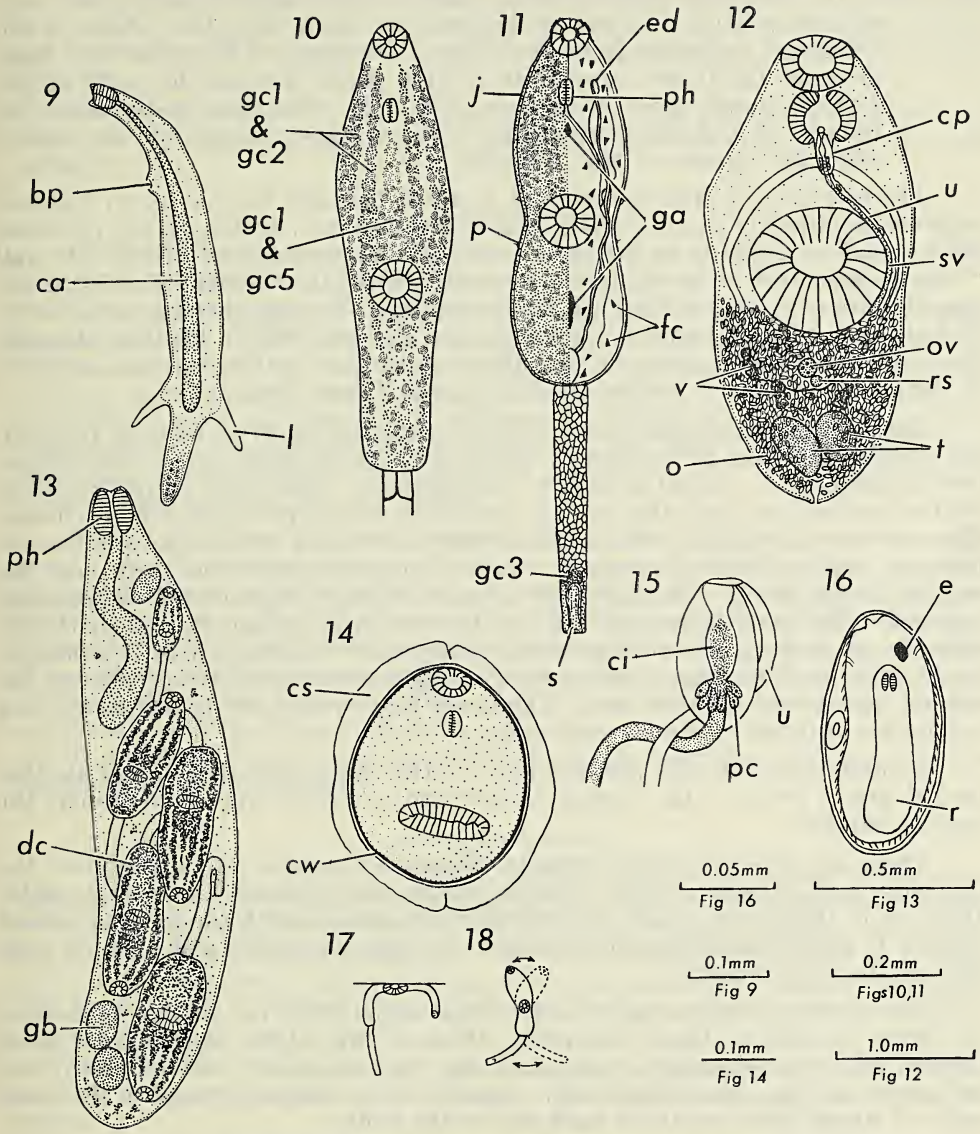
The more medial rows tend to merge with a triangular mass of cells between the pharynx and ventral sucker. Posterior to the ventral sucker, two lateral rows and one medial area, which is slightly less dense, are evident. Within these areas the various types of gland cells are disposed as follows :

(*a*) In longitudinal rows in forebody and in hindbody, large gland cells containing either rods (gc 1, Fig. 10) or large granules (gc 2, Fig. 10) ;



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(*a*) In longitudinal rows in forebody and in hindbody, large gland cells containing either rods (gc 1, Fig. 10) or large granules (gc 2, Fig. 10) ;

(*b*) in the triangular area between pharynx and ventral sucker, gland cells with rods (gc 1, Fig. 10) or fine granules (gc 5, Fig. 10). Prior to the release of cercariae from the rediae, the gland cells containing large granules (gc 2) are secreted to form a jacket around the body of the cercaria apart from the suckers (Fig. 11). The gland cells containing rods (gc 1) and fine granules (gc 5) do not appear to alter in disposition after the release of this material.

The secretion of granules to form a jacket has also been noted in *Fasciola hepatica* cercariae by Dixon (1966). These granules in *C. narrabeenensis* cercariae subsequently contribute to the outer cyst wall and, as this part of the cyst wall " tans " three to four weeks after cyst wall formation, it seems likely that the granules are of a similar chemical composition to the corresponding granules in *F. hepatica* cercariae, namely, tanned protein (Dixon, 1966). Further, the rods (gc 1) in *C. narrabeenensis* are probably comparable to the keratin scrolls of *F. hepatica* cercariae described by Dixon and Mercer (1964).

The average measurements of 10 free-swimming cercariae fixed in formalin are : body, 0·7 long by 0·2 wide ; tail, 0·44 long by 0·05 wide ; oral sucker, 0·07 in diameter ; ventral sucker, 0·1 in diameter. The body is constricted at ventral sucker level, and this is more noticeable in partly contracted specimens. There is a row of papillae at the anterior end ; associated with blocks of refractile material, and at least two sensory " hairs " on each side of the body near the ventral sucker level. The latter are almost obscured by secreted cystogenous material. The mouth, surrounded by the oral sucker, leads into a short prepharynx, 0·05 long, an oval muscular pharynx, 0·05 long, short oesophagus, 0·015 long, and the caecal bifurcation is approximately midway between the ventral sucker and anterior end. The caeca pass round the ventral sucker and extend to near the posterior extremity.

A small group of cells just posterior to the caecal bifurcation, and another medial group between the ventral sucker and excretory vesicle, represent the genital anlagen.

There are groups of cells, mostly obscured by rods, on each side of the forebody just anterior to the ventral sucker and between the caecal limbs. Ducts from these cells, which are probably comparable with the forebody gland cells of *P. burrili* cercariae and metacercariae, run anteriorly and open on each side of the oral sucker.

The excretory vesicle and anterior longitudinal ducts are similar to those in *P. burrili* cercariae. Each posteriorly directed limb of the longitudinal ducts divides into two secondary ducts near the ventral sucker, one of which runs anteriorly and the other posteriorly. Smaller ducts were not traced to the flame cells, of which there are 18 on each side of the body.

The tail is identical to the tail of *P. burrili* cercariae.

Metacercaria

(Fig. 14)

The cercaria fixes itself to the subtrate by the ventral sucker and the cyst is rapidly formed by the secretion of material from the remaining gland cells in the body using the jacket as a mould. The tail drops away almost immediately cyst wall formation commences. The metacercaria moves around inside the cyst, apparently shaping or smoothing out the interior surface. The cyst wall eventually appears to have at least two layers : an inner cyst wall proper and an outer flared layer cementing the cyst to the substrate. The outer layer has indentations at points corresponding to the anterior and posterior ends of the cercaria. When infected snails are confined to glass tubes the liberated cercaria appear to favour the operculum for encystment.

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The newly formed cyst is oval to round, 0·200 by 0·275. As mentioned above, the outer wall tans after three to four weeks, and once this has occurred the inner cyst can be separated from the outer cyst wall by compression with a coverslip.

The enclosed metacercaria appears to be very similar to the cercaria but lacks the cyst-forming gland cells. Excysted metacercariae have not been obtained.

Discussion

Of the six trematode species known to infect *Velacumantus australis* at their sporocyst or redial stage, the life histories of five have now been described.

To our knowledge, this is the first time that the life history of a *Cloacitrema* species has been described in any detail. That of *C. michiganensis* was discussed by Robinson (1952) but only a few details, unsupported by figures, were given. It is interesting to note that *C. narrabeenensis* n.sp. has a very similar life history to *Parorchis* spp., and indeed it is difficult to separate the megalurous cercariae of each genus. The presence of collar spines in *Parorchis* is perhaps the greatest difference between the two, but these are difficult to see. A further difference is the longer oesophagus in *Parorchis*.

The life history of *P. burrili* parallels the life histories of other species of the genus. As its cercaria is very similar to that of *C. narrabeenensis* and both are derived from rediae which infect *V. australis*, means of distinguishing them warrant mention. The fact that both species of cercariae encyst readily and the cysts differ considerably in shape permits an easy distinction to be made. Further, *C. narrabeenensis* cercariae are slightly larger and more opaque due to the presence of gland cells containing rods. These rods appear some time before the cercariae are mature and this, along with the caudal appendage present in rediae of *P. burrili*, enables distinctions to be made between the two philophthalmid infections encountered in *V. australis*.

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List of Abbreviations for Text-figures

bp—birth pore
c —caudal appendage
ca—caecum
ci —cirrus
cp—cirrus sac
cs —cementing substance of cyst
cw—cyst wall proper
dc—developing cercariae
e —eyespot
ed—excretory duct
ev—excretory vesicle
fc —flame cell
ga—genital anlagen
gb—germ ball
gc 1–gc 5—various types of gland cells referred to specifically in text
j —jacket
l —lappet
o —eggs
ov—ovary
p —papilla with sensory " hair "
ph—pharynx
pc—prostate cells
rs —receptaculum seminis
r —mother redia
sv —seminal vesicle
s —tail sucker
u —metraterm
t —testes
v —vitellaria
te—terminal excretory pore

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